

MIDDLE AND LATE JURASSIC MARINE REPTILE FAUNAS OF THE SOUTHEASTERN PACIFIC, BASED ON DISCOVERIES IN ARGENTINA AND CHILE

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ABSTRACT

The South American record of Jurassic marine reptiles complements the northern hemisphere record both geographically and stratigraphically. Middle Jurassic marine reptiles fill a gap from the Aalenian to the early Callovian, when the records are scarce or absent elsewhere. Early Bajocian ichthyosaurs from the Neuquén Basin document the co-occurrence of non-ophthalmosaurids and ophthalmosaurids and include the oldest record of Ophthalmosauridae. Similarly, the record of South American metriorhynchids is older than that of Europe. The oldest *Metriorhynchus* in Chile is early Bajocian, whereas in Europe, it is early Callovian. *Metriorhynchus aff. M. brachyrhynchus* in northwestern Patagonia is late Bathonian whereas the oldest *M. brachyrhynchus* in Europe is early Callovian. Early-Middle Jurassic plesiosaurs are extremely scarce worldwide, and *Maresaurus* from the early Bajocian represents almost the only plesiosaur of this age. The highest abundance and taxonomic diversity, however, occurs in the Late Jurassic (Tithonian) of the Neuquén Basin and includes pleurodiran and cryptodiran turtles (*Notomemys laticentralis* and *Neusticemys neuquina*), ophthalmosaurid ichthyosaurs (*Caypullisaurus bonapartei*, *Ophthalmosaurus sp.* and *Aegirosaurus sp.*), pliosaurs (*Pliosaurus sp.*, *Liopleurodon sp.*) and metriorhynchids (*Metriorhynchus sp.*, *Geosaurus araucanensis* and *Dakosaurus andiniensis*).

Jurassic marine reptile faunas from the Southeastern Pacific are closely related to Western Tethyan faunas. These close similarities can be explained in terms of a marine connection (Caribbean seaway) between both areas. The Caribbean seaway ("Hispanic Corridor") played an important role for dispersion of marine reptiles since the Middle Jurassic, or even before. Toward the end of the Jurassic in the European Tethys, mass extinctions diminished the diversity of marine reptiles. However, in the Southeastern Pacific (Argentina and Chile) no evidence suggests massive extinctions, at least in the record of marine reptiles.

INTRODUCTION

One important bias in the interpretations of Mesozoic marine reptile faunas is that they are mainly based on the record of the northern hemisphere. But, as Massare (1997) pointed out, to understand the diversity, biogeography and evolution of marine reptiles, it is very important to include data from southern oceans. Within this frame, the South American record of Jurassic marine reptiles is significant in that it complements the northern hemisphere record both geographically and stratigraphically. Thus, in the northern hemisphere, Early Jurassic and middle Callovian- Kimmeridgian times are well documented, whereas the early Middle Jurassic is poorly documented. By contrast, Early Jurassic marine reptiles are almost unknown from the Eastern Pacific margins of South America (this can be

explained in terms of uneven collecting efforts) (Fernández and Lanés, 1999), but significant material is known from the Aalenian- early Callovian. Concerning the Late Jurassic, the Tithonian herpetofauna of South America complements the one recorded in the northern hemisphere, and together, they demonstrate the diversity of pelagic reptiles of those times.

In 1994, we were invited by Dr. Elizabeth Nicholls and Jack Callaway to contribute to the book *Ancient Marine Reptiles* which was published few years later (Callaway and Nicholls, 1997). Our contribution was restricted to Tithonian marine reptiles of the Eastern Pacific (Gasparini and Fernández, 1997). Since that publication, new material has been found from the Middle and Late Jurassic (Gasparini and Fernández, 1997: fig. 2; and Figure 1) and the systematics of the groups involved has improved

		<i>Cayullisaurus</i>	<i>Aegirosaurus</i> sp	<i>Ophthalmosaurus</i> sp	<i>Geosaurus</i>	<i>Dakosaurus</i>	<i>Metriorhynchus</i>	<i>Notoemys</i>	<i>Neusticemys</i>	<i>Pliosaurus</i>	<i>Liopleurodon</i>	Localities
TITHONIAN	Late	█		█	█	█			█	█	█	Pampa Tril Trincajuera
	Middle		█					█	█			Los Catutos
	Early	█			█		█	█	█			Malargüe Cerro Lotena

A

		<i>Ophthalmosauridae</i>	<i>Mollesaurus</i>	<i>Stenopterygius cayi</i>	<i>Thalattosuchia</i> indet.	<i>Metriorhynchus</i>	<i>Maresaurus</i>	<i>Cf. Muraenosaurus</i>	<i>Cf. Cryptoclidus</i>	Localities
Callovian	Late									Qda Sajasa Chacaico Sur
	Middle									
	Early				█		█	█		
Bathonian	Late				█					Cachay Melelhue
	Middle									
	Early									
Bajocian	Late									Qda La Iglesia Chacaico Sur
	Early	█	█	█	█	█	█			
Aalenian	Late	█								Qda Remoredo
	Early									

B

FIGURE 1. Geographic and temporal distribution of Middle Jurassic and Tithonian marine reptiles in the Neuquén Basin. **A**, Middle Jurassic; **B**, Tithonian.

significantly (e.g. Motani, 1999 a,b; O'Keefe, 2001, 2002; Gasparini et al., 2006). The goal of the present contribution is to summarize and update the information on southeastern Pacific marine reptiles, and to analyze the significance of these faunas.

JURASSIC MARINE REPTILES FROM ARGENTINA AND CHILE

Jurassic reptiles of the southeastern Pacific come from Argentina and Chile. Chilean marine reptiles are recorded from the Sinemurian to the Tithonian, but are isolated and generally quite fragmentary (Figure 2A). In Argentina, they are concentrated in what is known as the Neuquén Basin (Spalletti et al., 2000; Howell et al., 2005) (Figure 2B, C). This basin encompasses an area of approximately 120,000 km², with extensive marine outcrops that range from the Jurassic to the Albian. The record of marine reptiles (see the main localities in Figure 2B), ranges from the Lias to the Tithonian (Gasparini and Fernández, 2005).

Middle Jurassic Discoveries—The first marine reptile from the Middle Jurassic was described by Cabrera (1939). He described a rostral fragment of a Bajocian ichthyosaur from Chacaico Sur, Argentina (Figure 2B) as the new species of *Stenopterygius*: *S. grandis* (Figure 3A). Due to the fragmentary nature of the specimen and the lack of diagnostic features, *S. grandis* was considered a *nomen vanum* by Gasparini (1985).

Nearly four decades later, Gasparini and Chong (1977) described a well preserved and complete skull of a Callovian crocodile from Quebrada Sajasa in northern Chile (Figure 2A), and they assigned it to a new species *Metriorhynchus casamiquelai*. This species was synonymized with *M. brachyrhynchus* (Adams-Tresman, 1987) and revalidated by Gasparini et al. (2000) (Figure 3B).

A few years later, Tavera (1981) described marine reptile remains of several specimens found in the early Bajocian of Quebrada La Iglesia, Chile (Figure 2A). He described them as ichthyosaurs, but Gasparini et al. (2000), referred some of the specimens to *Metriorhynchus* sp, this occurrence being the oldest record of the genus worldwide. The rest of the material described by Tavera (1981) has little taxonomic value, being assignable only to Ichthyosauria indet (Fernández, in press a)

In 1984, during geological prospecting in Quebrada Remoredo, Argentina (Figure 2B), a fragment of an ichthyosaur forefin was collected from the *Pulchenquia malarguensis* ammonoid zone (Aalenian-Bajocian boundary), Los Molles Formation (Figure 1B). This material remained undescribed at the

Museo de La Plata until 2003. It preserves the distal part of the humerus and the complete zeugopodium (Figure 3C). Anterior to the radius there is a well preserved extrazeugopodial element which supports two accessory digits. This zeugopodial pattern is diagnostic for Ophthalmosauridae, and the specimen therefore documents the presence of this taxon (Fernández, 2003).

During the 1990's, as result of several field trips within a framework of a research project on Mesozoic marine reptiles of South America, the authors and co-workers (Spalletti et al., 1994) recovered new material of these reptiles in the early Bajocian and early Callovian levels of the Los Molles and Lajas formations exposed at Chacaico Sur, Neuquén, Argentina (Figures 1B, 2B). From the early Bajocian levels of the Los Molles Formation, the most outstanding specimens are two ichthyosaurs and one pliosaur.

One of the ichthyosaurs (Figure 3D) was described as a new genus and species, *Chacaicosaurus cayi* Fernández, 1994, but was reassigned to *Stenopterygius cayi* by Fernández (in press a). This ichthyosaur is a long snouted form, with a forefin pattern consistent with the one described by McGowan and Motani (2003) as diagnostic of the genus *Stenopterygius*. The other ichthyosaur, *Mollesaurus periallus* Fernández, 1999 (Figure 3E), is a robust and large form. Phylogenetic analysis places *Mollesaurus* as an ophthalmosaurid, although its position within the clade cannot be resolved at this stage of knowledge (Fernández, in press b).

Maisch and Matzke (2000) considered *Mollesaurus periallus* a junior synonym of *Ophthalmosaurus icenicus*. We reject this proposal since comparable elements known in both species are quite different. One of the most conspicuous features of *Ophthalmosaurus* is the reduction of the postorbital region of the skull, a feature not present in *Mollesaurus*. The external nares in *Ophthalmosaurus* are curviform, whereas the nares are elongated in *Mollesaurus*. The basioccipital condyle is clearly set off from the extracondylar area in *Ophthalmosaurus* but not in *Mollesaurus*. Finally, the vertebral centra of *Mollesaurus* are long in comparison with the relatively short vertebral centra of *Ophthalmosaurus* (Fernández, in press a).

In the same locality, Chacaico Sur (Figure 2B) and stratigraphic level (early Bajocian), several remains of pliosaurs were found, among the most complete being a skull and mandible articulated referred to the new pliosaur taxon *Maresaurus coccai* Gasparini, 1997 (Figure 3F). According to a recent redefinition of Pliosauroida (O'Keefe, 2001) *Maresaurus* belongs to the rhomaleosaurids.

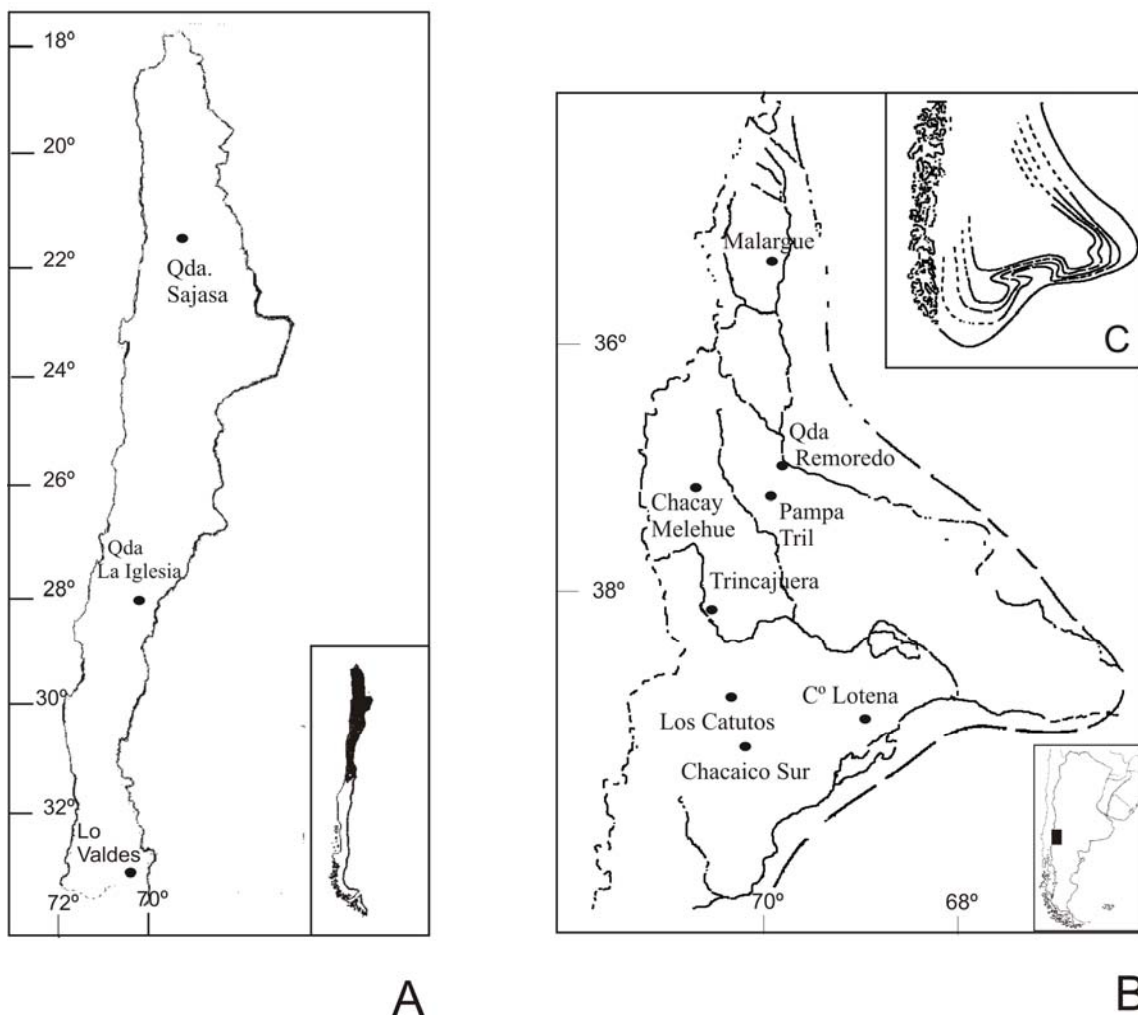


FIGURE 2. A and B, Location maps; A, Chile; B, Argentina. C, Reconstruction of the Nequén Basin modified from Spalletti et al. 2000.

The single record of a marine reptile in the late Bajocian of South America is the metriorhynchid *Metriorhynchus* aff. *M. brachyrhynchus* (Gasparini et al. 2005) found in Chacay Melehue, Neuquén (Figure 2B, 3G).

Finally, the youngest marine reptiles of the Middle Jurassic in western South America are the plesiosaurs from the early Callovian of north-western Patagonia and the metriorhynchids from the early-middle Callovian of northern Chile. In Chacaico Sur (Figure 2B) a few plesiauroid vertebrae were found, as well as numerous post-cranial fragments of plesiosauroids. Part of this material was referred to cf. *Muraenosaurus* (Figure 3H) and cf. *Cryptoclidus* (Gasparini and Spalletti, 1993) (Figure 3I). In northern Chile, *Metriorhynchus casamiquelai* and fragmentary remains referred to *Metriorhynchus* sp. were found (Gasparini et al., 2000).

Late Jurassic Discoveries—The first reports of marine reptiles of South America date from the end of the 19th century and comprise fragmentary remains of ichthyosaurs from different localities of northwestern Patagonia and rocks referred to the Late Jurassic. Based on these materials, the following new species were described: *Ichthyosaurus leucopetraeus* Burmeister and Giebel, 1861; *I. bondenbenderi* Dames, 1893; and *I. immanis* Phillipi, 1895. Due to the fragmentary state of the materials, their dubious provenance data, and because in some cases they were not illustrated and/or their repository could not be identified, the specimens could not be revisited. Consequently, the validity of these taxa was questioned by Gasparini (1985), who included them as *nomina vana*. Although these first records did not add significant data to the knowledge of the South

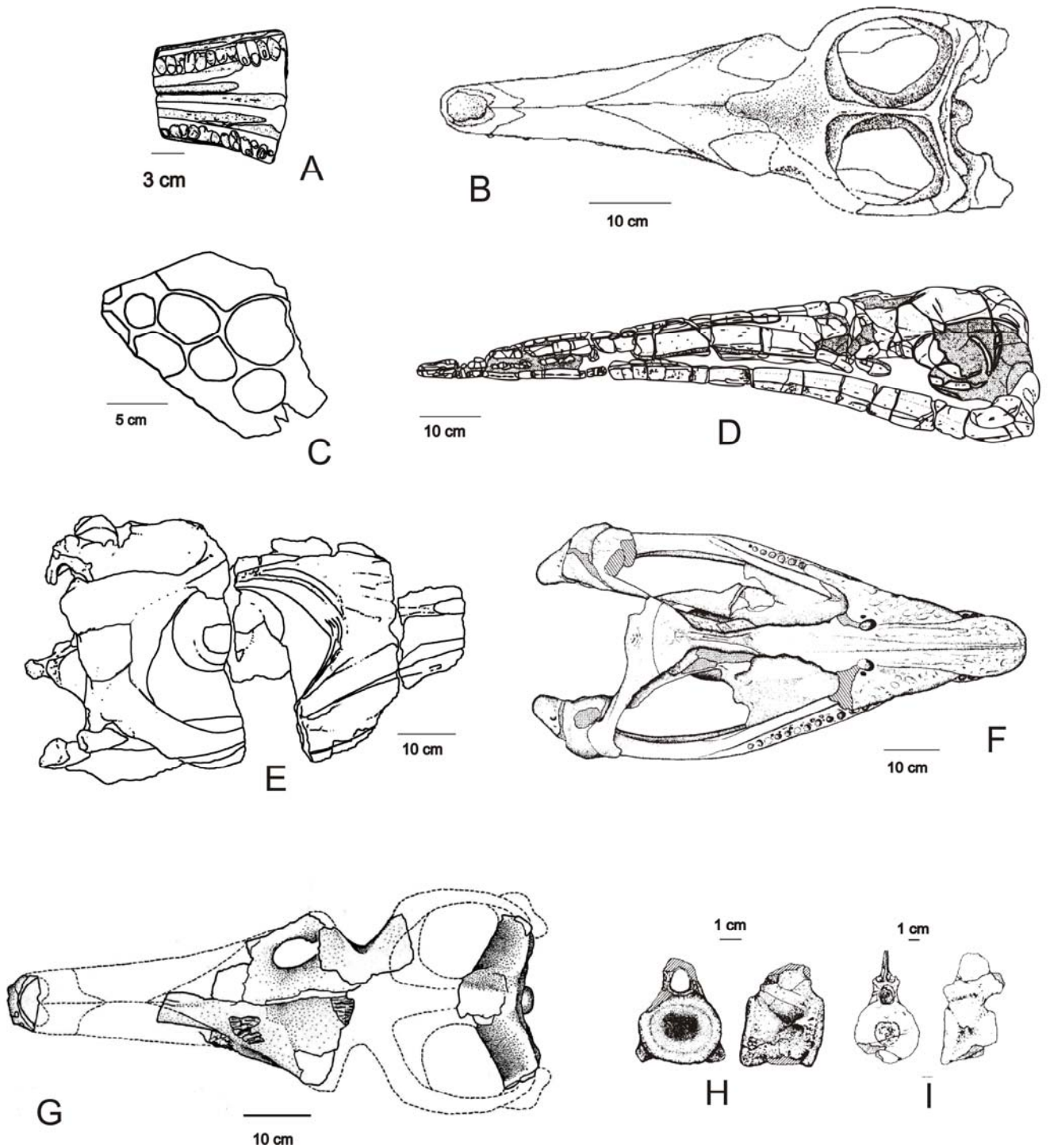


FIGURE 3. Middle Jurassic marine reptiles from the southern Eastern Pacific. **A**, “*Stenopterygius grandis*”, early Bajocian, Neuquén Basin; **B**, *Metriorhynchus casamiquelai* early Callovian, northern Chile; **C**, Ophthalmosauridae indet, Aalenian-Bajocian boundary, Neuquén Basin; **D**, *Stenopterygius cayi*, early Bajocian, Neuquén Basin; **E**, *Mollesaurus periallus*, early Bajocian, Neuquén Basin; **F**, *Maresaurus coccai*, early Bajocian, Neuquén Basin; **G**, *Metriorhynchus* aff. *M. brachyrhynchus*, late Bathonian, Neuquén Basin; **H**, cf. *Muraenosaurus*, early Callovian, Neuquén Basin; **I**, cf. *Cryptoclidus*, early Callovian, Neuquén Basin. (Modified from Gasparini and Fernández, 2005).

American marine faunas, they suggested the richness of the Jurassic deposits of Patagonia and guided further prospecting.

By the middle of the 20th century, Carlos Rusconi described marine reptile remains, mainly ichthyosaurs, found by himself in the Tithonian of the Vaca Muerta Formation in Mendoza province (Argentina). He assigned most of the ichthyosaur material to a new genus, *Ancanamunia* Rusconi, 1942, *A. mollensis* (Rusconi, 1938) and *A. mendozana* Rusconi, 1940; and as a new species of *Ichthyosaurus*, *Ichthyosaurus inexpectatus* (Rusconi, 1948a). The dental morphology and distribution of the alveoli suggest that the material referred to *I. inexpectatus* belongs neither to an ichthyosaur nor to a plesiosaur. This material might belong to a large crocodylian, probably *Dakosaurus* sp. (Vignaud and Gasparini, 1996). Rusconi (1948b) also described a new species, *Purranisaurus potens*, and referred it to Plesiosauria, but Gasparini (1985) assigned it to the metriorhynchid *Metriorhynchus potens*. However, the type material needs preparation and revision, and it was recently referred to *Metriorhynchus* sp. (Pol and Gasparini, in press).

As in the case of Middle Jurassic marine reptiles, the knowledge of Late Jurassic material has improved significantly during the last 20 years. Except for one vertebra from Lo Valdes (Chile) (Figure 2A), all Late Jurassic fossils have been found in Tithonian levels of the Vaca Muerta Formation exposed in several localities of northwestern Patagonia (Figure 2B, C). In decreasing order of abundance, marine reptile fossils belong to ichthyosaurs, metriorhynchids, turtles and pliosaurs.

Most of the ichthyosaurs found in the 1990's have been identified as *Caypullisaurus bonapartei* Fernández, 1997 (Figure 4A). This species has been recorded in early, middle and late Tithonian levels of the Vaca Muerta Formation. The richest localities in number of discoveries are Cerro Lotena (early Tithonian) and Yesera del Tromen-Pampa Tril (late Tithonian) (Figure 1, 2B). The presence of *Ophthalmosaurus* was documented by an isolated forefin found in the late Tithonian of Trincajuera creek (Fernández, 2000). Recently two skulls and forefin elements (Figure 4 B) confirmed the presence of the genus in the Tithonian of the Vaca Muerta Formation (Fernández and Cocca, 2004). One ichthyosaur found in the middle Tithonian of Los Catutos (Figure 4C) is referable to the genus *Aegirosaurus* (MF, pers.obs.). Finally, a juvenile from the same locality (Museo Olsacher de Zapala -MOZ 1854), previously identified as *Ophthalmosaurus monocharactus* (Gasparini, 1988), is also under revision and probably corresponds to a new taxon of Ophthalmosauridae (Figure 4D). Maisch and Matzke (2000:fig.8) referred this specimen to *Aegirosaurus*

Bardet and Fernández, 2000, but comparable diagnostic elements preserved in *Aegirosaurus* and in MOZ 1854 do not justify Maisch and Matzke's (2000) proposal (Fernández, in press a).

All Late Jurassic marine turtles from the southern Eastern Pacific can be assigned to two taxa: *Notoemys laticentralis* (Pleurodira) (Figure 4E) and *Neusticemys neuquina* (Cryptodira) (Figure 4F). *Notoemys laticentralis* is known from three well preserved specimens which were found in early and middle Tithonian levels of Cerro Lotena and Los Catutos, while six specimens of *Neusticemys neuquina* have been found in early, middle, and late Tithonian levels of the Vaca Muerta Formation exposed at Cerro Lotena, Los Catutos and Trincajuera creek (Figure 2B; de la Fuente and Fernández, 1989; Fernández and de la Fuente, 1988, 1993, 1994).

Plesiosaurs of the Late Jurassic are all pliosauroids, found in the early and late Tithonian Neuquen Basin of northwestern Patagonia (Figure 1A, Figure 2B). Although the fossils are well preserved, as are most reptiles of this age in the Neuquén Basin, they are still insufficiently studied, and in most cases lack a final preparation. Preliminarily, they were referred to *Pliosaurus* sp., *Liopleurodon* sp. (Figure 4G), and to Pliosauridae (Figure 4H; Gasparini et al., 1997; Spalletti et al., 1999; Gasparini, in press). However, the validity of *Liopleurodon* is still controversial (O'Keefe, 2001; Noè et al., 2004).

Crocodyliforms of the Late Jurassic in southern Eastern Pacific are all metriorhynchids, and except for a single vertebra found in Lo Valdés, Chile (Figure 2A), were found in the Vaca Muerta Formation (Tithonian) in the provinces of Mendoza and Neuquén (Figure 2B). While a single specimen is currently referred to *Metriorhynchus* sp. (see *Purranisaurus*), most belong to the longirostran *Geosaurus araucanensis* Gasparini and Dellapé, 1976 (Figure 1A, Figure 4I). Recently, a rostrum referred to *Dakosaurus andiniensis* Vignaud and Gasparini, 1996 (Figure 2B, Figure 4J), has been found. However, the extreme brevirostry in that species was demonstrated by the discovery of an almost complete skull with mandible, in Yesera del Tromen/Pampa Tril (Figure 2B; Gasparini, et al., 2006).

Although they are not strictly marine forms, pterosaurs flew over the Tithonian seas of the Neuquén Basin. So far, they are scarce and incomplete but they suggest the presence of Pterodactyloidea (*Herbstosaurus pigmaeus* Casamiquela, 1975). Another specimen, the most complete Jurassic pterosaur as far known from South America, appears closely related to the Archaeopterygidae (Codorniu and Gasparini, in press; Codorniu et al. 2006).

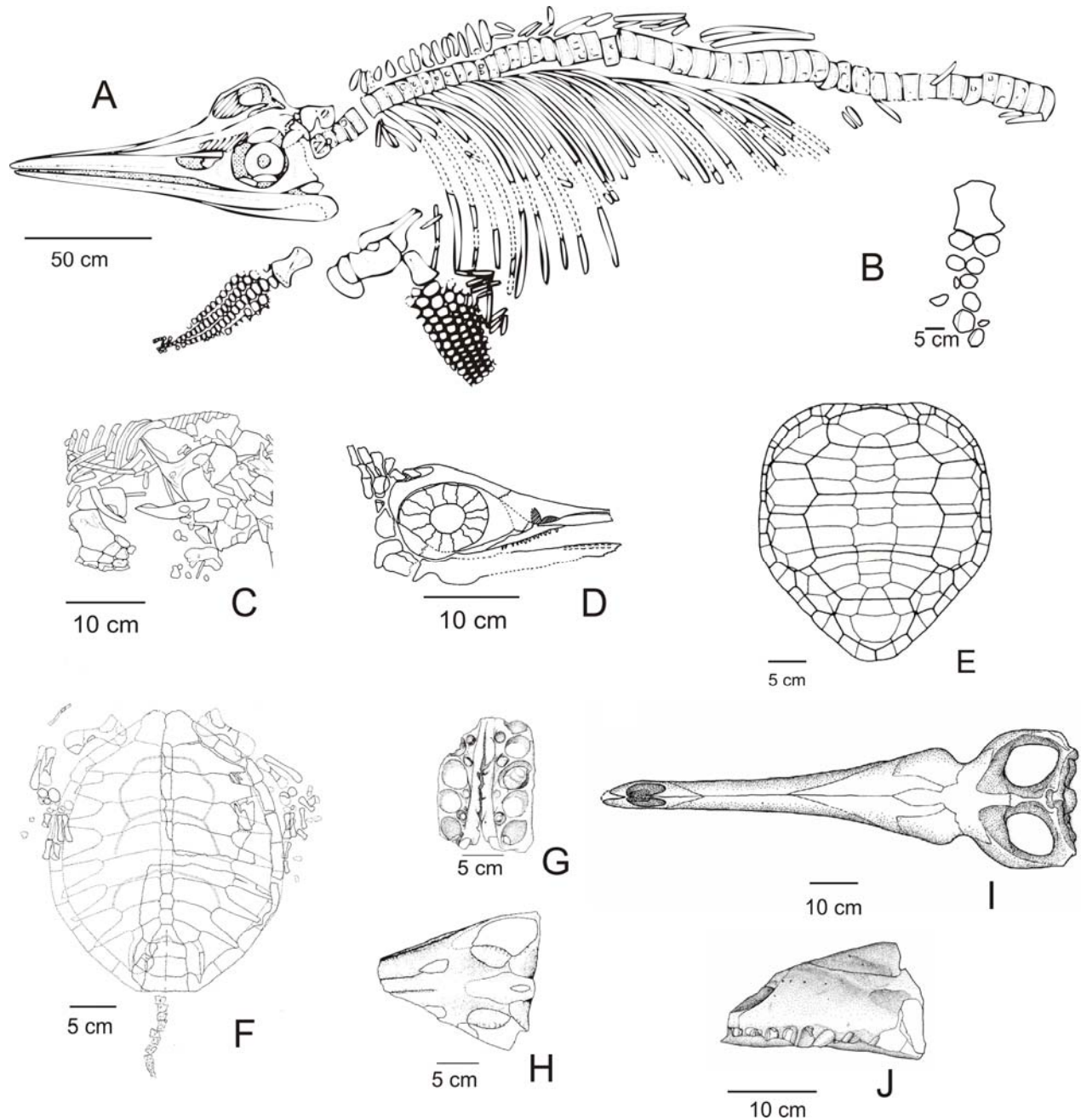


FIGURE 4. Tithonian marine reptiles from the southern Eastern Pacific (Neuquén Basin). A, *Caypullisaurus bonapartei*; B, *Ophthalmosarus sp.*; C, *Aegirosaurus sp.*; D, Ophthalmosauridae; E, *Notoemys laticentralis*; F, *Neusticemys neuquina*; G, *Liopleurodon sp.*; H, Pliosauridae; I, *Geosaurus araucanensis*; J, *Dakosaurus andiniensis*. (Modified from Gasparini and Fernández, 2005).

SIGNIFICANCE OF JURASSIC MARINE REPTILE RECORD FROM THE SOUTH-EASTERN PACIFIC

Middle Jurassic—Middle Jurassic marine reptiles in the southern Eastern Pacific are significant as they fill a gap from the Aalenian up to the early Callovian, when the records are scarce (plesiosaurs, metriorhynchids) or absent (ichthyosaurs) elsewhere

(Bardet, 1995; Vignaud, 1995; McGowan and Motani, 2003). Although not very diverse so far, the marine herpetofauna of the southern Eastern Pacific documents a poorly known period in the evolution of marine reptiles communities.

Marine reptiles found in early Middle Jurassic levels of the Neuquén Basin are off-shore predators. In the particular case of ichthyosaurs, they are significant

for the following reasons: (1) they interrupt a hiatus of 14 my; (2) they document the co-occurrence of non-ophthalmosaurids and ophthalmosaurids; (3) one of them (Figure 3C) represents the oldest record of Ophthalmosauridae extending back the biochron of the clade by 12 my, and showing that the presence of an extrazugopodial element was acquired as early as the Aalenian-Bajocian boundary (Fernández, 2003).

As for ichthyosaurs, the record of South American metriorhynchids is older than that of European ones. The record of *Metriorhynchus* in Chile is from the early Bajocian, whereas in Europe, it is from the early Callovian (Gasparini et al. 2000). Similarly, *Metriorhynchus* aff. *M. brachyrhynchus* in northwestern Patagonia is recorded in the late Bathonian (Gasparini et al. 2005) whereas the oldest record of *M. brachyrhynchus* in Europe is from the early Callovian of France (Vignaud, 1995).

Early-Middle Jurassic plesiosaurs are extremely scarce worldwide, and *Maresaurus* from the early Bajocian represents almost the only plesiosaur of this age. The holotype is well preserved, with an almost complete skull. It displays a mix of characters present in the Early Jurassic (*Rhomaleosaurus*) and Middle Jurassic (*Simolestes*) rhomaleosaurids (Gasparini, 1997; Gasparini in press).

Finally, both the Callovian metriorhynchids of Chile (*Metriorhynchus casamiquelai*) and the plesiosauroids of Argentina (cf. *Muraenosaurus*; cf. *Cryptoclidus*) are related to forms that lived during those times in the European Tethys.

Based on the main Lagerstätten of the European Jurassic, a major reorganization event was proposed for the Middle Jurassic, namely the replacement of an ichthyosaur-dominated fauna during the Early Jurassic by a pliosauroid/crocodile-dominated one (Massare 1997). However, as Massare (1997) pointed out, how real is the observed variation in diversity? The record of marine reptiles in the European basins is poor between the end of the Toarcian and the middle Callovian, approximately 11 Ma. The marine reptiles from the Eastern Pacific partially fill that gap and suggest the Aalenian-Bajocian to Callovian as a gradual period of transition. Thus, there are typical "Early Jurassic elements" represented by *Stenopterygius cavi*, "Early-Middle Jurassic elements" as *Maresaurus*, "Callovian /post Callovian elements" as *Mollesaurus*, Ophthalmosauridae indet (Figure 3C), *Metriorhynchus*, and cf. *Muraenosaurus* and cf. *Cryptoclidus*.

Close similarities between Jurassic Eastern Pacific and Western Tethyan faunas (i.e. the presence of *Metriorhynchus* and *Stenopterygius* in both faunas) can be explained in terms of a marine connection between both areas. The use of a Caribbean seaway ("Hispanic Corridor") for dispersion of marine reptiles

since the Middle Jurassic, or even before, has been proposed by Gasparini (1985, 1992, 1996) and Gasparini and Fernández (1996, 1997). Some authors (e.g. Aberhan, 2001; Damborenea, 2000) used the term "Hispanic corridor" for this Caribbean connection and suggested that before the Late Jurassic it acted as a filter allowing the passage of on-shore species. In agreement, geological evidence suggests that during the Middle Jurassic, the Caribbean seaway was not a true "corridor" which implies a full communication and faunal interchange, but an intercontinental channel system allowing connections only temporally during high sea level stands (Iturralde-Vinent, 2004). Based on this, Gasparini and Iturralde-Vinent (in press) restricted the term "Hispanic Corridor", implying a full connection and faunal interchange, to the Caribbean seaway since the Oxfordian. Nevertheless, the role played by the Caribbean seaway could not be exactly the same for marine invertebrate distribution (such as bivalves) as for marine reptiles. Thus, the presence of an intercontinental channel system before the Oxfordian (i.e. during the Middle Jurassic) could have been a "corridor" for marine reptiles while being a filter for the dispersion of forms such as bivalves. Thus, for ichthyosaurs, metriorhynchids, and plesiosaurs, because of their independence of the substrate and their swimming capabilities, such a passage could permit a full interchange, although intermittent, between Western Tethys and Eastern Pacific during the Early–Middle Jurassic.

Late Jurassic—The most abundant marine reptiles of the Late Jurassic of the southern Eastern Pacific are ichthyosaurs. Until the 1990's, Late Jurassic ichthyosaurs had been considered abundant but not diverse (McGowan, 1991). Recent collection and research has shown that ichthyosaurs were not only abundant, but that diversity was higher than previously thought. Thus, in the Tithonian of the Neuquén Basin at least three different genera have been recorded: *Ophthalmosaurus* sp., *Aegirosaurus* sp. and *Caypullisaurus*.

The only thalattosuchians of the Late Jurassic in the southern Eastern Pacific are the metriorhynchids *Metriorhynchus* sp., *Geosaurus araucanensis* and the brevirostrine *Dakosaurus andiniensis*. This species is characterized by an extremely high and narrow snout with a few, large teeth with serrated edges, which suggests habits of a top predator and reveals that morphological and ecological diversity of marine crocodyliforms was much wider than previously thought (Gasparini et al. 2006).

All the plesiosaurs of the upper Jurassic of the Neuquén Basin are pliosaurids, including specimens whose skull reached 2.50 m long. Although validity of *Liopleurodon* is under debate (Noè et al. 2004), forms

referable to the classically defined *Pliosaurus* sp. and *Liopleurodon* sp. are identified.

Turtles found in the Vaca Muerta Formation documented an important event in the secondary adaptation of Testudines to marine environments. Nicholls (1997) suggested three separate radiations of marine turtles: the earliest, comprised only Jurassic cryptodiran turtles (“plesiochelydis”) living in shallow and coastal waters; the second radiation, during Cretaceous and Tertiary, correspond to pleurodiran pelomedusoids, and the third radiation corresponds to the chelonoids, with their oldest record in the early Cretaceous. Jurassic turtles from the Neuquén Basin, however, suggest that the earliest radiation comprised not only cryptodirans but pleurodirans as well. While *Notoemys* “maintained” the typical locomotive apparatus of a continental turtle, *Neusticemys* shows strong modifications in its limbs, the most conspicuous being the general elongation of the forelimb (e.g. the length of the forelimb is approximately 60% the length of the carapax). Besides carapace and limb bones, *Notoemys* displays no special adaptation to life in the sea. Indirect evidence, however, suggests that these turtles inhabited marine environments. *Notoemys* has been found in the marine Tithonian sediments of three different localities of the Neuquén Basin, none of the specimens show evidences of *post mortem* transport from continental environments, and moreover, two of them preserved articulated limb elements. If we considered as “marine reptile” any reptile able to grow and feed in salt water environments (Hua and Buffetaut, 1997), then *Notoemys* is a marine turtle. In addition, *Neusticemys* exhibits limbs with striking modifications. The humerus preserves a primitive pattern but the manus has a significant elongation and its hind limb is not reduced. This pattern is currently unique to Patagonian turtles.

Toward the end of the Jurassic there were mass extinctions (Raup and Sepkoski, 1988), and within the European Tethys, the diversity of marine reptiles diminished together with the shallowing of the basins (Bardet, 1995). However, in the southern Eastern Pacific there is no evidence suggesting massive extinctions, at least in the record of marine reptiles. On the contrary, the same taxa are recorded in the same localities both in the Tithonian and the Berrisian (*Geosaurus araucanensis*, *Dakosaurus andiniensis*, *Caypullisaurus bonapartei*, *Liopleurodon*). It is not until the Valangian, when the south of the Neuquén Basin became shallower, that the marine herpetofauna began to change. Then, only elasmosaurid plesiosaurs are recorded in coastal environments (Lazo and Cichowolsky, 2003).

Toward the end of the Jurassic Laurasia and Gondwana were defined, with the opening of new seaways that would have facilitated the dispersion

and/or yearly migration of pelagic forms. Large pliosauroids (*Liopleurodon*, *Pliosaurus*), metriorhynchids (*Geosaurus*, *Dakosaurus*), and ichthyosaurs (*Ophthalmosaurus*, *Aegirosaurus*) in the European Tethys and the southern Eastern Pacific suggest close paleobiogeographic relationships.

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